

SCOPUS

SURVIVAL AND INTERCOLONY MOVEMENTS OF
WHITE-BROWED SPARROW WEAVERS
PLOCEPASSER MAHALI

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From 17 March to 17 June 1976, we ringed 45 White-browed Sparrow Weavers *Plocepasser mahali* with individual combinations of coloured rings and, in some cases, with aluminium rings as well, in the Samburu-Buffalo Springs Game Reserve, Kenya; 26 in seven colonies at the Samburu Game Lodge area and 19 in four colonies near the Buffalo Springs bandas. The natural vegetation is largely acacia wooded grassland. A map showing the location of 13 nesting colonies at Samburu has been published with details of behaviour (Collias & Collias 1978a).

SURVIVORSHIP

Each colony had its nests in an acacia tree. During 6-12 April 1978 (Collias & Collias 1978b) and again from 6-10 September 1980 we returned to the two study sites to look for surviving individuals. In April 1978 we found 21 (47 per cent) of the colour-ringed birds still present after two years. None of the young fledged during the breeding season of 1976 apparently survived these two years, and all but one disappeared within three months of age. In September 1980 we found 11 birds (24 per cent) of those ringed in 1976, still present after a period of just over four years. The birds had the same combination on both legs and colour ring loss was not serious during the first two years (Collias & Collias 1978b), while enough rings persisted so that all but one survivor could be identified in 1980. The high survivorship minimized the importance of ring loss.

We found that 21 of 43 birds ringed as adults in 1976 survived the first two years, and were still present in the study area, while of these 21 survivors, 11 survived to September 1980. If the probability of an individual dying during any one month is q then the probability of surviving one year is $(1-q)^{12}$. From this formula (R. Vance, pers. comm.) we calculated the average annual survival. The annual survival of birds ringed as adults in 1976 averaged 70 per cent during the first two years and 77 per cent from April 1978 to September 1980. These figures are rather similar to the figure for adult annual survival for *P. mahali* found by Lewis (1980) for two years in mopane woodland in northeast Zambia of 74 per cent and 69 per cent, and indicate high survival rates for adults in this species. Like ourselves, Lewis checked for movements of colour-ringed birds beyond a peripheral zone of colonies surrounding the study area and also found very little, if any, such movement, indicating that disappearance of birds was probably largely, if not entirely,

due to mortality rather than to emigration. We checked for ringed birds in 14 neighbouring colonies 50-150 m from the ringing sites, and all were unringed except for movement of ringed birds one to two colonies away from a ringed colony. We were generally able to census all the birds within a colony within one hour, but repeated the census in doubtful cases.

MOVEMENTS AND RESIDENCE

The birds reside at their colonies the year round, and defend a group feeding territory about 50 m in diameter around the acacia tree in which their nests are located. In 1978, after two years, 11 of 20 colour-ringed survivors had moved from their original home to an adjoining territory (7 birds), or to a colony only two territories removed (4 birds), while the remaining nine still lived in the same colonies. But in 1980, nine of the 11 survivors from birds ringed in 1976 still resided on the same territories as in 1978, and only two birds had moved to an adjacent territory. It would appear that attachment to a given colony became firmer after two years, while more shifting took place during the first two years after being ringed as adults.

Male YO was found in the same colony in 1976, 1978 and 1980, and each year appeared to be the most dominant bird in this colony. In a neighbouring colony, Male AY was the most dominant bird in 1976 and 1978, but had disappeared by 1980, his place as dominant male being taken by Male AB. Male AB was originally ringed two territories away in 1976, and he circulated between three different colonies in 1978 when he slept in the colony adjoining the one in which he was found in 1980. Male BB was repeatedly and almost constantly attacked by the dominant male of the colony in which he was ringed in 1976, and BB eventually left this colony for another in which he was found in both 1978 and 1980.

In each colony of *P. mahali* there was only one brood female who did all the incubating and most of the feeding of the young. Female AA left her home colony for another colony two territories removed in which she was found to be the brood female in both 1978 and 1980. In 1978, on the same day as she was incubating, Female AA was seen to feed nestlings in another colony two territories away. In that colony, Female GR became the brood female, after the original brood female of 1976 disappeared, and Female GR was apparently the brood female both in 1978 and 1980, though not in 1976 (although she was then a colony member).

COLONIES AND POPULATION DENSITY

Territorial boundaries remained essentially the same, with few exceptions, in some 27 colonies observed over the period of 4½ yr, despite turnover of most of the population. Thus, territorial boundaries were traditional, and their locations survived the individuals composing the colonies. The same trees were often used in boundary disputes between neighbouring groups in 1976, 1978 and 1980.

Between 1976 and 1978, one colony at Samburu Lodge became extinct, apparently because of human disturbance, while one new colony appeared. By 1980, the colony that had become extinct was replaced by one in a tree next to the original colony tree. The birds prefer isolated trees for their nests. At Buffalo Springs, between 1976 and 1978, the birds of one colony moved their nests over to another tree about 12 m away after the canopy of the original colony tree and that of two adjoining trees grew to overlap.

The strong territorial behaviour of *P. mahali* appears to exert considerable stabilizing influence on population density, but at Samburu there was an increase in population size of over 40 per cent between 1976 and 1980. In 18 Samburu colonies, in April 1976, April 1978 and September 1980, we counted in all 88, 110 and 126 adults and fledged young, respectively. The average number

of adults per colony in each of these three years was 5, 6 and 7 respectively. The year 1976 was relatively dry and survival of the young was generally poor. Most breeding takes place during the rains, but some young may be raised even during the dry season. In September 1980, towards the end of the long dry season, we saw three fledged young at the Samburu Lodge site and one at the Buffalo Springs bandas area.

To summarize: 1) Over a period of about 4½ yr, *P. mahali* populations showed a high annual adult survival, and the population density and average colony size increased by about 40 per cent. 2) The birds are sedentary and the location of colony trees and of territorial boundaries generally outlast the life of the individuals composing the populations. 3) About half the ringed birds moved to neighbouring or other nearby colonies during the first two years after ringing, but the great majority remained in the same colonies from the second to the fourth year.

DISCUSSION

One of the nearest relatives of *Plocepasser* is *Pseudonigrita*. In April-June 1978 we colour-ringed 56 individuals of the Grey-capped Social Weaver *Pseudonigrita arnaudi* at the Olorgesailie National Prehistoric Site some 70 km south-west of Nairobi. In September 1980 we and Dr Derek Pomeroy found only six ringed individuals still present, and only one of these had been certainly ringed as an adult. However, of 29 adults which we had colour-ringed, Mr G.R. Cunningham-van Someren observed 14 (48 per cent) still present about 9 months later, equivalent to an annual survival rate plus dispersion out of the study area, of about 38 per cent for adult *P. arnaudi*, much less than the 70-80 per cent average annual survival indicated for adult *Plocepasser mahali*. It is possible that many of the birds dispersed widely in *P. arnaudi*. *Pseudonigrita arnaudi* is a smaller bird, weighing about 20 g compared to an average 42 g for *P. mahali*, and correlated with its apparently greater population turnover rate it usually lays three eggs to a clutch instead of the two characteristic of *P. mahali*. *Pseudonigrita arnaudi* does less communal feeding of the nestlings than does *P. mahali* (Collias & Collias 1980). Its maximum life span in nature is probably shorter since only six of 56 ringed individuals were found after 2½ yr in contrast to 11 of 45 *P. mahali* still alive after 4½ yr. The greatest maximum age we found for any of our colour-ringed individuals was 2 years and 10 months for *P. arnaudi* and 5 years and 4 months for *P. mahali*. Another closely related species, *Philetairus socius* the Sociable Weaver of southwestern Africa, is often put into the same subfamily, the Plocepasserinae, with the two preceding genera. Based on extensive ringing at the Kalahari Gemsbok National Park in South Africa, Maclean (1973: 232) thought it "unlikely that the Sociable Weaver's maximal longevity ever exceeds about 3½ years." It resembles *Pseudonigrita arnaudi* and differs from *Plocepasser mahali*, in addition to its shorter life, in usually laying a larger clutch (four eggs), and in that communal feeding of nestlings is less common than in *P. mahali*.

Plocepasser mahali resembles many small land birds of tropical regions and differs from most of those of temperate and colder regions in high survival of adults, in relatively long life once adulthood is reached, in having an enclosed nest, in laying a very small clutch of eggs (usually two), and in that more than two birds usually feed the nestlings and fledglings. The relatively long life span of adults may be a key factor in this complex of differences from small land birds of temperate or colder zones. Survival rates for adults of most species of small temperate zone land birds range between 40 to 60 per cent (Ricklefs 1969, Cody 1971). In contrast, Snow & Lill (1974) have reported annual adult survival rates of 70 to 90 per cent for 15 species of ringed forest birds of various species of the New World tropics in Trinidad, and Fogden (1972) of 86 per cent for various land birds, excluding hole

nesters, of the Old World tropics in Sarawak. One would expect greater average adult survival of small land birds in the tropics than in the temperate or colder zones because the hazards of migration and seasonal cold are much less in the tropics. Many species of tropical birds lay small clutches, and one reason for this may be that high adult survival means fewer places available for young birds. Fewer young birds are needed to replace a long-lived adult population. Communal nesting with more than two birds caring for the brood, is much more common in the tropics than in higher latitudes (Rowley et al. 1976). Here again, in the face of a saturated population, with many long-lived adults, one of the best evolutionary strategies that young birds could adopt would be to help their parents raise younger brothers and sisters, until they could establish a place for themselves as independent breeders. Brown (1974) and Woolfenden (1976) have expressed similar views for communal nesting jays of warm temperate latitudes, as has Fry (1980) after a survey of the world literature comparing longevity in tropical and temperate zone birds. Fry points out that, "scant as tropical studies have been, small land birds of low latitudes commonly attain the advanced ages known for only a tiny fraction of high latitude birds." Brown & Pomeroy (in press) have developed data from tropical Africa which indicate that large birds generally live longer than small birds, and that communal or co-operative breeders tend to live longer than species where only the mated pair raises the young.

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